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Spatial variation in fish species richness on coral reefs: habitat fragmentation and stochastic structuring processes

Timothy R. Ault and Craig R. Johnson

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Most studies of coral reef fish communities have been restricted to site-attached species on small, isolated patches of habitat. Few have investigated spatial variation in fish species richness in relation to predictions based on stochastic or deterministic processes of community organisation. Our aims were to: (1) compare species richness on contiguous and fragmented reef habitats, and (2) investigate the mechanisms underlying spatial variation in species richness. Quantitative comparison of species-area curves for contiguous and patchy coral reef indicated that patch reefs support more species than equivalent areas of contiguous reef. However, Monte-Carlo simulated rarefaction curves indicated little difference in the species-individuals relationship for both habitats. Rarefaction was employed to eliminate variation in species richness among sites due to differences in sample size (number of fish present). After removal of sample-size effects, multiple regression models explained 30% and 25% of total variability in species richness on contiguous and patchy coral reef based on variation in habitat structure (e.g., depth, shelter availability, substratum characteristics). To investigate the likely importance of stochastic processes in determining spatial variation in species richness, we compared the species-individuals relationship from contiguous reef sites with the relationships derived from null models involving the random reallocation of fish among sites. Comparisons of the observed data with the outcomes of the null models indicated that spatial variation in species richness was not wholly attributable to stochastic processes. We suggest that the observed patterns of species richness may reflect species interactions (e.g., competition and predation) within fish communities.

T. R. Ault and C. R. Johnson, Dept of Zoology, Univ. of Queensland, Queensland 4072, Australia (present addresses: TRA: Australian Water Quality Centre, Private Mail Bag 3, Salisbury, SA 5108, Australia [tim.ault@sawater.sa.gov.au]. – CRJ: Dept of Zoology, Univ. of Tasmania, GPO Box 252-05, TAS 7001, Australia).

Many tropical communities, including fish communities on coral reefs, are characterised by high species richness and diversity, and a principal goal of community ecology has been to identify the mechanisms that maintain this diversity (Connell and Orias 1964, Pianka 1966, MacArthur and Levins 1967, Ehrlich 1975, Sale 1977, Connell 1978; reviewed by Rosenzweig 1995). Maintenance of high species richness has been attributed to a variety of processes including biotic interactions, such as 'present' or 'past' competition (Connell 1980) and predation (Ayal and Safriel 1982, Caley 1995); physical disturbances (e.g., Connell 1978); and stochastic demographic processes (Sale 1977). However, for coral reef fish communities, the significance of each of these mechanisms remains unclear. Here, we investigate the likely processes structuring coral reef fish communities by examining spatial patterns in species richness across two reefs on the southern Great Barrier Reef.

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Hypotheses explaining the structure and dynamics of coral reef fish communities can be broadly categorised as based on deterministic or stochastic processes. Early ecologists interpreted the great abundance and high morphological and taxonomic diversity of coral reef fish communities as evidence that coral reef fish assemblages were deterministic in nature (Odum and Odum 1955, Hiatt and Strasburg 1960, Smith and Tyler 1972, 1973, Smith 1978). High population densities and resource limitation (food or space) were presumed to lead to strong competition, resulting in high rates of speciation and niche diversification. This view was centred around the importance of species interactions in community dynamics, i.e., competition for limiting resources and interactions between predators and prey.

In contrast, alternative models (principally Sale's 'lottery' hypothesis, Sale 1974, 1975, 1976, 1977, 1978, 1979; and the recruitment limitation hypothesis, Williams 1980, Doherty 1981, 1983, Victor 1983, 1986, Doherty and Fowler 1994a, b; see Doherty and Williams 1988) imply that the structure of fish communities fluctuates spatially and temporally in response to stochastic patterns of colonisation (via settlement and recruitment of pelagic larvae) and extinction. The lottery hypothesis asserts that total fish abundance is limited by space on the reef but that space is partitioned stochastically among species according to priority of arrival, i.e., when a resident adult dies, the vacant habitat is colonised by a random individual from a multi-species pool of potential recruits. Competitive exclusion does not occur because the members of ecological guilds (containing functionally similar species) are equal in competitive ability and residents cannot be displaced by invading individuals.

Competitive exclusion is also unimportant in the recruitment limitation model but for different reasons. Under recruitment limitation, the overall magnitude of recruitment is insufficient to cause resource limitation. Thus, competition does not occur and consequently, spatial and temporal variability in species abundance is dependent on variation in recruitment.

Apart from the work of Sale (1974, 1975, 1976, 1979) which led to the development of the lottery hypothesis, few researchers have examined the richness and/or diversity of coral reef fish communities in relation to predictions derived from models of community dynamics. The principal aim of our study is to investigate spatial variability in species richness across two coral reefs and compare the patterns observed with those expected on the basis of stochastic lottery processes or recruitment limitation. Predicted patterns of spatial variation in species richness based on both models would be similar, but the nature of these patterns would depend on the spatial distribution of fish larvae immediately before settlement. If larvae are distributed homogeneously, then the observed spatial variability in species richness should not differ from that obtained from the random placement of individuals among sites (Sale and Douglas 1984, Sale and Steel 1986; see also McGuinness 1984, Hart and Horwitz 1991). However, if settlement processes are spatially heterogeneous so that the distribution of larvae of particular species are aggregated at some scale (see Breitburg 1991), observed measures of species richness will be lower than estimates based on a random placement model because individuals settling at each site are more likely to belong to the same species. To examine both predictions, we construct two null models to simulate stochastic processes under regimes of spatially uniform and heterogeneous recruitment. The first (random placement model) is based on the random redistribution of individual fish among sites, while the second (group placement model) is based on the random reallocation of groups of individuals. The results of both models are compared with the observed data to assess the adequacy of stochastic processes in explaining the observed patterns.

The second objective of the study is to compare spatial variation in species richness among sites on patchy and contiguous coral reef. Comparisons of this type enable quantitative assessment of the effects of patch size and habitat fragmentation on species richness, and assessment of whether conclusions drawn from patch reef studies can be extrapolated legitimately to fish communities on contiguous reef (Walsh 1985, Jones 1987a, 1988, Robertson 1988, Sale 1991, Sale and Guy 1992, Sale et al. 1994).

The main difficulty in comparing species richness among contiguous and patch reef sites stems from the non-linear accumulation of species with area (McGuinness 1984, Williamson 1988, Hart and Horwitz 1991, Rosenzweig 1995). Species richness cannot be compared directly among sites of different areas, and indices of species diversity (based on both the number and proportional abundance of species) are similarly influenced by variation in sample size (Magurran 1988, Hart and Horwitz 1991, Rosenzweig 1995). In this study, we use two statistical approaches to account for sampling artefacts associated with the accumulation of species with increasing area or numbers of individuals. In the first, the slope of the species-area curve for patch reefs is compared with the slopes estimated for contiguous reef sites to investigate the rate at which species accumulate with area on the two habitats. In the second, we use rarefaction to adjust for variation in sample size before comparing species richness among sites on contiguous and patchy reef.

Methods

Study sites and survey methods

Field work was conducted at Heron and Wistari Reefs (23°21′ S, 151°55′ E) in the Capricorn Group, southern Great Barrier Reef, Australia. Both are platform reefs

and consist of a shallow lagoon which is surrounded by an inner and outer reef flat, reef crest, and outer reef slope. All sampling was carried out on the reef slope at depths of 4 to 15 m. On most sides of both reefs, the outer slope is formed by large tracts of contiguous reef. However, areas of the northern slopes of both reefs are patchy in nature, formed primarily by isolated outcrops of coral (patch reefs) which vary in size and extent of isolation from neighbouring patches.

Between October 1992 and October 1993, a total of 36 sites (each 100 m^2) on contiguous reef and 39 patch-reef sites (0.3 to 60 m^2) were surveyed for fish community and habitat structure. At sites on contiguous reef, fish species abundance was recorded within a 10×10 m grid of 25 quadrats, each measuring 2×2 m. Each quadrat was surveyed for 2 min by a single diver (TRA) on SCUBA. All fish within 3 m of the substratum were recorded, with the exception of small cryptic species, nocturnal species, and semi-pelagic species not usually associated closely with the substratum. Species which form large schools were also excluded from the analysis as accurate counting of these species is difficult, and habitat selection and movement by schooling fish are largely dependent on the position of neighbouring individuals (see Sale 1980, Sale and Douglas 1981, DeMartini and Roberts 1982, Ault and Johnson 1998). The same survey method was used for patch reefs, except that a smaller grid of 2×2 m quadrats was applied as the area of each patch was less than 100 m^2. The fish survey method is described in greater detail in Ault and Johnson (1998).

At each site, habitat characteristics were measured, including depth, topographic complexity and compositional diversity of the substratum, live coral cover, shelter availability, and reef connectivity (patch reef sites). Topographic complexity was defined as $TC = (L_s - L_d)/(L_d)$, where L_d is the straight line length across the site, and L_s the 'surface length' obtained by running a tape as closely as possible over the contours of the substratum (Risk 1972, Luckhurst and Luckhurst 1978, Sale and Douglas 1984). Parallel transects assessing topographic complexity were taken at 2-m intervals across each site.

Assessment of the compositional diversity of the substratum was based on the relative cover of several substratum categories. Coral substrata (live and dead) were classified by growth form, and included encrusting, digitate, branching, tabulate, massive, and soft coral. Non-coral substrata included rubble (coral fragments less than 5 cm in diameter), and sand (fragments and particles less than 0.5 cm in diameter). Percentage cover of each substratum category was estimated visually for each 2×2 m quadrat and the estimates averaged to obtain a mean description of substratum composition. A measure of substratum diversity was obtained using the Shannon Index: $H' = \Sigma\, p_i \ln(p_i)$, where p_i is proportion of the total area covered by the ith substratum type.

Shelter availability was measured by counting the number of holes that had a depth equal to or greater than the minimum diameter of the entrance. Holes were placed in three size categories according to minimum entrance diameter: (1) small (3–10 cm), (2) medium-sized (10–20 cm), and (3) large (>20 cm). For each size class, an estimate of hole density was calculated by averaging the counts from each 2×2 m quadrat.

For patch reef sites, connectivity (degree of isolation from neighbouring patches) was estimated using an index of connectivity (C_t) (see Ault and Johnson 1998). Connectivity in a single direction (C) was estimated by recording the presence or absence of suitable reef habitat at 1-m intervals over a 30×2 m belt transect radiating out from the patch. Following measurement, C was calculated as:

$$C = \sum_{i=1}^{d} a_d \,(\arctan(r/d)\pi)$$

where r is the radius of the patch and a_d is a binary parameter indicating the presence ($a_d = 1$) or absence ($a_d = 0$) of reef at a distance d along the transect. As most patch reefs sampled were approximately circular or elliptical, r was estimated from patch area assuming each patch was circular. An average estimate of connectivity in all directions (C_t) was obtained by averaging C from eight belt transects radiating out from the site at 45° angles (N, NE, E, SE, S, SW, W, NW).

Analysis of species-area curves

For patch reef sites (which ranged in area from 0.3 to 60 m^2), number of species observed (S) was plotted against the area of the site (A) and a power relationship ($S = CA^Z$) was fitted by least-squares regression. For each contiguous reef site, a species-area relationship was generated by estimating the average number of species encountered over the site at five different spatial scales: 4, 12, 20, 48, and 100 m^2. This was possible because although contiguous reef sites were of identical size (100 m^2), they were composed of 25 quadrats each measuring 2×2 m. At the 4-m^2 scale, the number of species counted in each 4 m^2 quadrat were averaged over the 25 quadrats sampled. At the 12-m^2 scale, the average number of species encountered was estimated by randomly selecting 100 subsets of 3 quadrats (combined area 12 m^2) and averaging the number of species present in each subset. The same method was used for the 20- and 48-m^2 scales except that subsets of 5 and 12 quadrats were chosen. The number of species encountered over 100 m^2 equalled the number of species observed over the entire site (25 quadrats). Thus, for each contiguous reef site, a species-area curve was estimated as if we had sampled the site randomly at five different scales. Power relationships were fitted to species-area curves for all sites.

To investigate species richness relative to area sampled on contiguous and patchy reef, parameters of the species-area curve (transformed to linearity, i.e., $\log S = z \log A + \log C$) were compared with those estimated for the contiguous reef sites. The null hypotheses were that the slope (z) and intercept ($\log C$) of the species-area relationship for patch reef sites were derived from the populations of z and $\log C$ obtained from analyses of contiguous reef sites. Both null hypotheses were tested using a modified two-tailed t-test (Sokal and Rohlf 1995: 227).

Rarefaction analysis

The technique of rarefaction was first proposed by Sanders (1968) to yield expected numbers of species in samples of different sizes (number of individuals) based on the relative abundances of species in the total species pool. However, Sanders' original method has been criticised for its assumptions (Hurlbert 1971, Fager 1972, Simberloff 1972). Therefore, to obtain robust estimates of rarefied species richness, we used Monte-Carlo simulations of a random sampling strategy. In this procedure, individuals were selected at random from the total pool of individuals counted and the cumulative total of new species encountered was recorded. Random removal of individuals continued without replacement until all individuals had been removed. Simulations were repeated 250 times and mean rarefaction curves were plotted separately for contiguous and patchy reef habitats.

For each site on contiguous and patchy reef, the expected number of species was estimated by interpolation of the respective rarefaction curves. From this, the 'rarefaction residual' was calculated by subtracting the expected from the observed number of species. Residuals were standardised for sample size by dividing by the expected number of individuals. Standardised residuals were used as a *relative* indicator of species richness among sites containing different numbers of fish; the larger (more positive) the residual, the more species were present relative to the number expected. Thus, standardised residuals represent a measure of species richness after removal of the effect of sample size.

To examine the influence of habitat structure on spatial variation in species richness on contiguous and patchy reef independent of sample size, stepwise multiple regression (α to enter and remove variables = 0.15) was used to predict standardised rarefaction residuals (dependent variable) from habitat characteristics (independent variables). For contiguous reef sites, bivariate scatterplots of habitat data indicated that most habitat variables satisfied assumptions of normality, linearity, and homogeneity of variance. One variable, density of small holes, required transformation to $\log(x)$ to meet these assumptions. For the analysis of patch reef sites, patch area required transformation to $\log(x)$.

Null models of species richness on contiguous reef

Two null models were constructed to simulate fish communities structured by stochastic processes. In both analyses, fish were randomly redistributed among sites and species-individuals relationships were calculated from these randomised data. Both models were based on contiguous reef sites to avoid statistical artefacts due to the reallocation of fish among patch reefs of different areas.

The first null model (random placement model) simulated spatial variation in species richness among sites assuming that recruitment is homogeneous over the area in which the sites were located, i.e., the spatial distribution of recruits was random and non-aggregated. Under this recruitment regime, both lottery and recruitment limitation processes would produce patterns equivalent to a random placement model (McGuinness 1984, Sale and Douglas 1984, Sale and Steel 1986, Hart and Horwitz 1991). In the random placement routine, each fish in the total species pool (from all contiguous reef sites) was reallocated to a new site at random such that the final numbers of individuals at each site (I) were in accordance with the original numbers observed. Randomisations were repeated 2000 times and a power relationship ($S = CI^Z$) was fitted by least-squares regression to the species-individuals curve from each randomisation procedure. After transformation to linearity, the slope (z) and intercept ($\log C$) of the species-individuals relationship from the observed data were tested against the populations of z and $\log C$ from the 2000 analyses of randomised data. Significance was determined by direct comparison of the observed values with the null distributions from the randomised analyses (see Manly 1991, Potvin and Roff 1993).

The random placement model was used to compare the observed data with those expected on the basis of spatially homogeneous recruitment. However, it is possible that fish communities could be organised by lottery or recruitment limitation processes but that spatial heterogeneity in recruitment obscures the patterns expected from random placement. If recruits exhibit aggregated distributions, the mean number of species at each site will be less than that expected from random placement because individuals at each site will more frequently belong to the same species. To test this, an alternative null model, termed the group placement model, was constructed which preserved the spatial heterogeneity present in the observed data. In the group placement procedure, each column in the original data matrix (columns of species and rows of sites) was reshuffled such that the observed counts of each species (cell contents) were reallocated randomly to a new site. Thus, the total numbers of individuals at each site were not conserved but spatial variation in the distribution and abundance of each species was maintained. At

Table 1. Percentage of total fish counted by family.

Family	Contiguous reef sites	Patch reef sites
Pomacentridae	72.8	66.9
Labridae	16.4	21.5
Chaetodontidae	2.8	1.9
Scaridae	1.7	1.4
Acanthuridae	1.4	1.7
Other	4.9	6.6

completion of this process, a power relationship was fitted to the data on the number of species and number of individuals. Randomisations were conducted 2000 times, and the results were compared with the analysis of observed data in the same way as for the random placement model.

Results

Excluding nocturnal, cryptic, and schooling species, a total of 140 species and 18 393 individuals were counted at 36 contiguous reef sites, and 120 species and 5000 individuals were counted at 39 patch reef sites. Fish communities of both habitats were dominated by damselfishes (Pomacentridae) and wrasses (Labridae), with other families comprising relatively minor proportions of the overall community by number (Table 1).

Analysis of species-area curves

The power curve $S = 3.175A^{0.672}$ explained most of the variance in the relationship between species richness (S) and area (A) on patch reef sites ($r^2 = 0.79$; Fig. 1). Similarly, power curves fitted to the species-area relationships estimated for each contiguous reef site were characterised by high r^2 values, ranging from 0.962 to 0.997. A two-tailed t-test indicated that the slope (z) of the species-area relationship for patch reef sites was significantly greater than those estimated for contiguous reef sites ($t = 2.82$, df = 35, $P < 0.05$; Fig. 1). There was no significant difference between the intercept (log C) for species-area curves based on patch reef and contiguous reef sites ($t = -0.69$, df = 35, $P > 0.05$; Fig. 1). Thus, patch reefs tended to accumulate more fish species with area than comparable sections of contiguous reef.

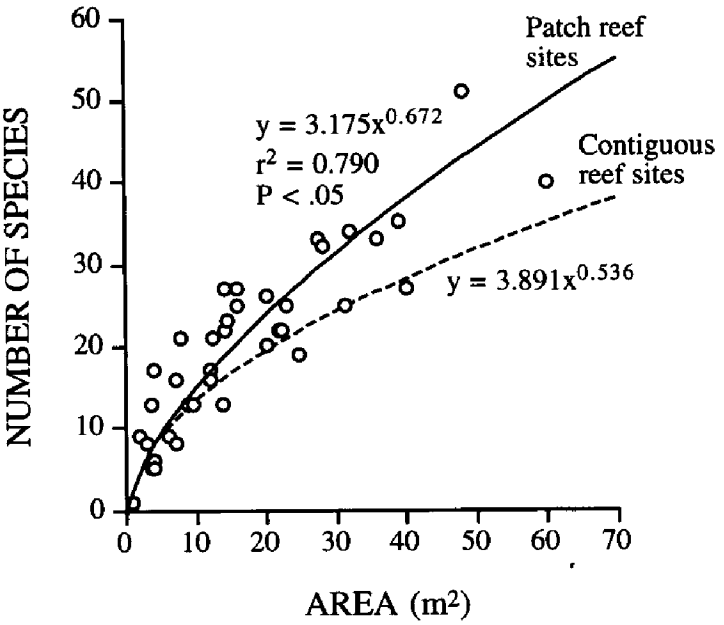

Fig. 1. Power curve fitted to species-area relationship for patch reef sites (solid line and open circles) and mean curve estimated for all contiguous reef sites (dashed line).

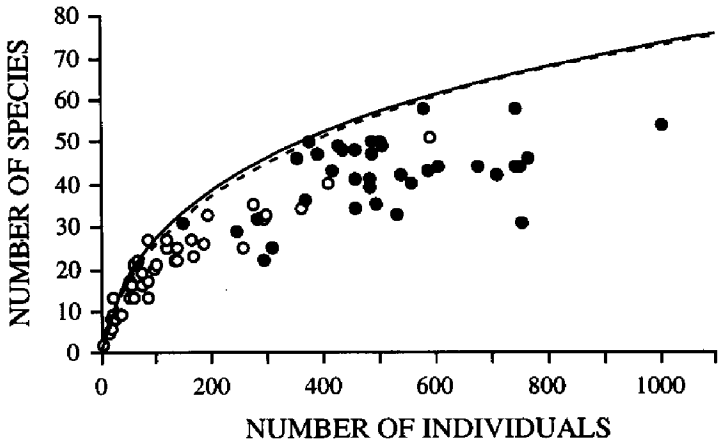

Fig. 2. Computer-generated rarefaction curves for contiguous reef (dashed line) and patchy reef habitats (solid line), and observed number of species and individuals for contiguous reef sites (dark circles) and patch reef sites (open circles).

Rarefaction analysis

While there was a significant difference in the species-area relationships for fish assemblages on contiguous and patchy coral reef, computer-simulated rarefaction indicated similar non-linear relationships between the cumulative number of species and number of individuals for contiguous and patch reef sites (Fig. 2). Previous researchers have attempted to linearise species-individuals relationships by applying logarithmic, power, or asymptotic transformations (DeCaprariis et al. 1981, McGuinness 1984, Williamson 1988). We applied each of these transformations to the rarefaction curves but all failed to produce a Gaussian distribution of residuals with linear regression. The slopes of the rarefaction curves depend on the distribution of species abundances, and thus, will be subtly affected by the degree of evenness or dominance in the community.

The magnitude of evenness or dominance in community structure is indicated by patterns of species abundance by rank. These patterns were very similar for the fish communities on patchy and contiguous reef (Fig. 3). Furthermore, rank abundances of the 25 most common species (comprising approximately 90% of the total community by number) on contiguous and patchy reef were significantly correlated, indicating little differ-

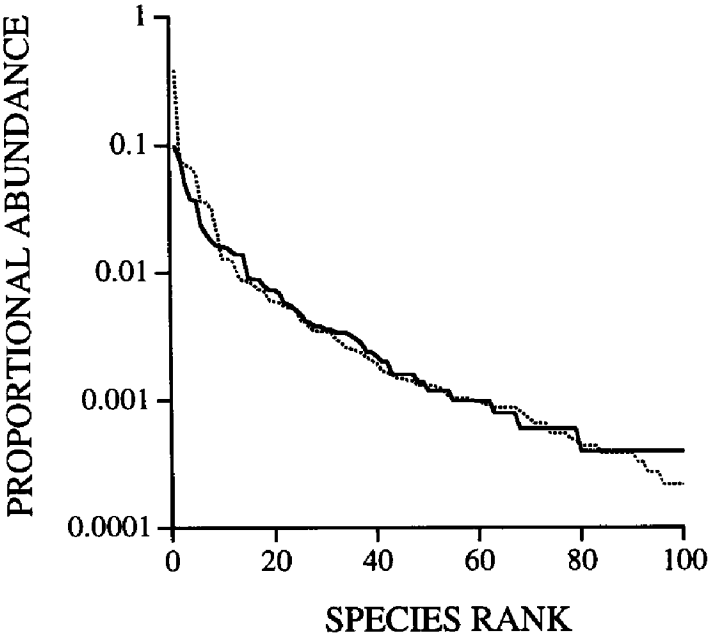

Fig. 3. Proportional abundance of the 100 most common fish species (ordered by numerical rank) on contiguous (dotted line) and patchy reef (solid line).

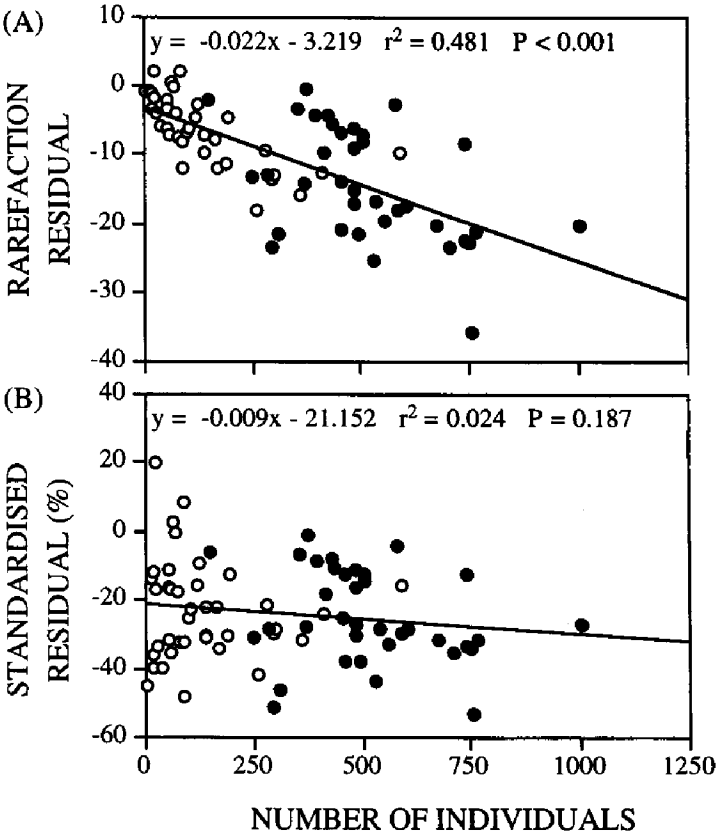

Fig. 4. Plot of rarefaction residuals (A) and standardised residuals (B) against number of individuals (sample size) for each contiguous (filled circles) and patch reef site (open circles). Standardised residuals are expressed as a percentage of the total number of individuals expected.

ence between habitats with respect to the relative abundances of common species (Spearman's $r_s = 0.782$; $P < 0.05$).

For all sites, with the exception of three patch reefs, the observed number of species was less than that predicted by the respective rarefaction curves (Fig. 2). There was also a trend of increasing negative residuals as sample size (number of individuals at the site) increased (Fig. 4A). This relationship was an artefact of sampling at different spatial scales and indicated the need for standardisation to prevent the analysis being dominated by large sites, e.g., in relative terms, a rarefaction residual of −10 species for a sample where 20 species are expected is more significant than a residual of −15 species for a sample where 60 species are expected. Standardisation of rarefaction residuals by the expected number of species effectively removed the bias in the survey data due to sample size (Fig. 4B). Standardised residuals were expressed as a percentage of the number of species expected, e.g., a residual of −50% indicated that the observed number of species was 50% less than the number expected for a given site.

To compare the effects of habitat structure on the species richness of fish assemblages on contiguous and patch reef sites, standardised rarefaction residuals were used to indicate species richness relative to the number of individuals counted. The larger (or least negative) the residual, the more species were observed relative to the number of individuals sampled. *R*-squared values for stepwise regression models predicting standardised residuals from habitat characteristics were similar for both contiguous and patch reef sites. For contiguous reef sites, 30% of total variation in rarefaction residual ($P = 0.008$) was explained by three habitat characteristics: proportion of live coral substratum, density of medium-sized holes, and depth (Table 2). Regression coefficients indicated that rarefaction residuals increased (became increasingly positive) with increasing

Table 2. *R*-squared, intercept, and regression coefficients for stepwise regression models predicting standardised rarefaction residuals for contiguous and patch reef sites from habitat variables. Habitat variables are listed in order of entry into regression models. * = Significant at $P < 0.05$; ** = Significant at $P < 0.01$.

Model	r^2	*Y* intercept	Habitat variable	Regression coefficient
Contiguous reef	0.30**	−32.96	% live coral	−0.39
			medium holes	2.83
			depth	1.18
Patch reef	0.25*	−27.87	depth	2.51
			patch area	6.78
			H' (substratum)	−24.94

depth and density of medium holes, and decreased as the proportion of live substratum increased (Table 2). For patch reef sites, 25% of total variation in rarefaction residual ($P = 0.017$) was explained by depth, patch area, and compositional diversity of the substratum (substratum H') (Table 2). On patch reefs, rarefaction residuals increased with increasing depth and patch area but decreased as the compositional diversity of the substratum increased (Table 2).

Comparison of observed data with null model predictions

The random placement model (based on the random redistribution of individual fish among sites) and the group placement model (based on the random reallocation of species counts among sites) both produced species-individuals curves which differed significantly from the observed data on contiguous reef (Fig. 5). Power curves fitted to the species-individuals data from 2000 iterations of the random placement model explained more variability (mean $r^2 = 0.83$; $P < 0.05$) than the relationship for observed data ($r^2 = 0.28$; $P < 0.05$). More importantly, the slope (z) of the species-individuals relationship for observed data was significantly less than the population of slopes from the analyses based on random placement of individuals (Fig. 6A).

The model based on the randomisation of species counts among sites (group placement model) resulted in poor relationships between number of species and number of individuals (mean $r^2 = 0.04$; $P > 0.05$ in

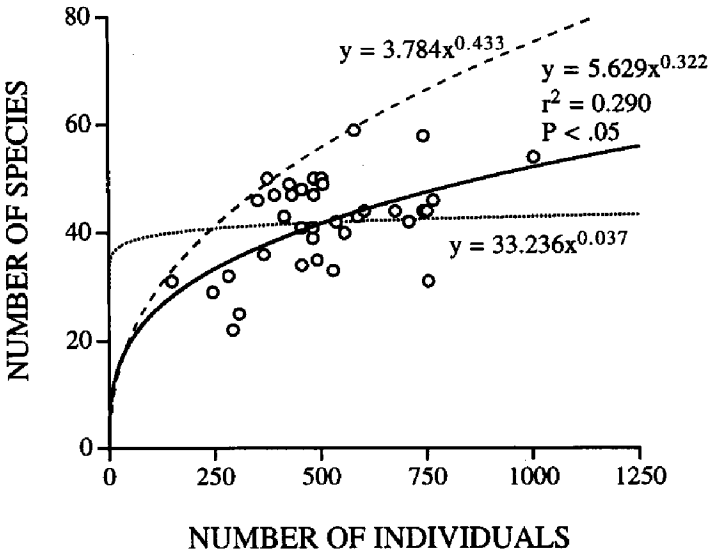

Fig. 5. Power curves summarising relationships between number of species and number of individuals. Solid line: relationship fitted to observed data from 36 sites on contiguous reef (open circles). Dashed line: mean relationship from 2000 randomisations reallocating individual fish among sites (random placement model). Dotted line: mean relationship from 2000 randomisations reallocating species counts among sites (group placement model).

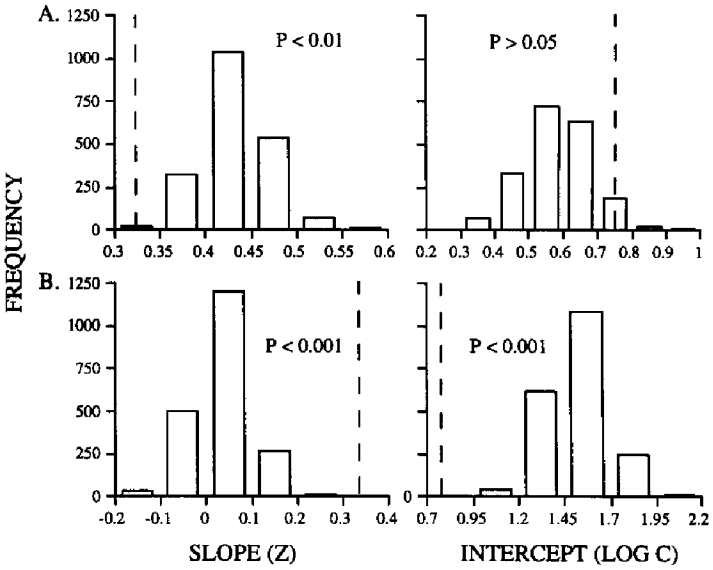

Fig. 6. Tests of the slope (z) and intercept (log C) from the species-individuals power relationship from observed data (dashed lines) and 2000 sets of randomised data (frequency histograms): (A) randomisation of individual fish among sites (random placement model), (B) randomisation of species counts among sites (group placement model).

over 90% of cases; Fig. 5). Also, differences in z and log C between observed data and randomised data were highly significant (Fig. 6B). For the large majority of analyses of randomised data, z was not significantly different from zero ($P > 0.05$; mean $z = 0.037$; Fig. 5) indicating no relationship between species richness and the number of individuals among sites of equal area.

Overall, neither null model produced patterns of variation in species richness similar to those observed among contiguous reef sites. For the random placement model, estimates of species richness were consistently and significantly higher than those observed. For the group placement model, there was no relationship between species richness and the number of individuals present on contiguous reef sites.

Discussion

Comparison of species richness on contiguous and patchy reef

Analysis of species-area curves indicated that the slope of the species-area relationship was significantly higher for patch reef sites than for contiguous reef sites, i.e., there was a higher rate of encounter of new species on patchy reef than on contiguous reef as the area of survey increased. This pattern is unlikely to be related to habitat differences between sites on contiguous and patchy reef. Ault and Johnson (1998) found that on the reef slope of Heron and Wistari Reefs, contiguous and patch reef sites were similar in habitat structure. The only exceptions were that contiguous reef sites tended to contain significantly higher proportions of branching coral and rubble (5–10%), while patch reef

sites were slightly deeper (mean difference 0.2 m) and contained an increased proportion of dead coral rock and a higher density of medium-sized holes (mean difference 0.7 holes m^{-2}).

The difference in the species-area relationship for contiguous and patch reef sites may be due to edge effects associated with the size of patch reefs. Much of the surface area of small patch reefs is bordered by sand, offering an attractive habitat for species that utilise sandy substrata but require nearby reef for shelter. As patch reefs increase in size, an increasing proportion of the patch is located centrally, surrounded by reef. Consequently, larger patch reefs may attract species that utilise reef habitat in addition to those species associated with edge habitats. In contrast, fish assemblages inhabiting sites on contiguous reef, which were not situated near large areas of sand, lacked species exhibiting a strong preference for sandy substrata. The absence of these species may have led to a lower species richness on contiguous reef compared to large patch reefs. On patch reefs, a number of sand-associated species were recorded that were rare or absent from contiguous reef sites, e.g., *Gymnocranius audleyi* (Lethrinidae), *Xyrichtys pavo* (Labridae), *Parapercis hexophtalma* (Pinguipedidae), and *Parupeneus barberinus* (Mullidae).

While empirical species-area relationships differed between patchy and contiguous reef habitats, rarefaction curves relating number of species to number of individuals were similar for both habitats. This apparent paradox is explained by the dissimilar nature of the two types of data. For typical communities with a log-normal distribution of species, species richness is strongly influenced by the number of rare species in the sample. In contrast, rarefaction curves of large, pooled samples reflect both the number of species and the relative abundance of species (evenness) and, thus, are a more reliable indicator of overall species diversity. The similarity in rarefaction curves reflects the close correspondence in the composition of pooled fish faunas on contiguous and patchy reef. Therefore, while the presence and abundance of rare species may have varied between habitats, the relative abundance of common species did not.

Effects of habitat structure on species richness

To examine the effects of habitat structure (i.e., depth, substratum characteristics, shelter availability, patch area and reef connectivity) on the species richness of fish assemblages, we constructed multiple regression models to predict 'rarefaction residuals' for sites on contiguous and patchy reef. In both models, a significant proportion (30% and 25%) of spatial variation in species richness (independent of sample size) was attributable to variation in habitat structure. However, the habitat variables included in the models differed for sites on contiguous and patchy reef. On contiguous reef, proportion of live coral, availability of medium-sized holes, and depth explained most variation in rarefied species richness, while on patchy reef, depth, patch area, and compositional diversity of the substratum were most important (Table 2). Other studies investigating relationships between fish species richness and habitat structure have also identified variability in the importance of particular habitat characteristics. Positive correlations have been demonstrated between species richness and a number of habitat measurements, including topographical complexity of the substratum (Risk 1972, Luckhurst and Luckhurst 1978), biological diversity of the substratum (Roberts and Ormond 1987), depth (Roberts and Ormond 1987), and proportion of live coral (Bell and Galzin 1984). Variability in the apparent importance of particular habitat characteristics probably reflects divergent responses by different fish species in different habitats, e.g., contiguous vs patchy reef. Ault and Johnson (1998) found that for 15 common fish species on Heron and Wistari Reefs, the structure of fish assemblages (species composition and abundance) on contiguous reef is largely dependent on intrinsic habitat characteristics (e.g., depth, composition of the substrata, shelter availability). In contrast, the structure of fish assemblages on patchy reef is primarily related to the degree of reef fragmentation.

The correlations between fish species richness and habitat structure identified in our study require careful interpretation. On contiguous reef, rarefied species richness tended to increase with increasing depth and density of medium-sized holes, and decrease with increasing cover of live coral (Table 2). On patch reefs, rarefied species richness was positively correlated with both depth and patch size (Table 2). The latter correlation would result if there were increases in the rates of colonisation and decreases in the rates of local extinction with increases in patch size, in accordance with classical dynamics of island biogeography (MacArthur and Wilson 1967; see also Simberloff 1976, Harrison 1991). Similar patterns were observed by Molles (1978) who documented species colonisation and turnover on artificial patch reefs.

For the patch reef sites examined in this study, there was a significant negative correlation between species richness and the compositional diversity of the substratum. Given that some fish species inhabiting coral reefs demonstrate specialised habitat use, a positive correlation might be expected, i.e., the number of habitat types within a site may regulate the number of 'habitat specialists' present. While positive relationships between species richness and habitat heterogeneity may exist at large scales (10^2–10^3 m; see Roberts and Ormond 1987) they do not appear to be important for reef fish at local scales (10^0–10^1 m). On sites offering highly heterogeneous substrata at local scales, the small frag-

mented patches of habitat may be insufficient to attract habitat specialists, leading to lower levels of species richness.

Mechanisms underlying spatial variation in species richness

The observed pattern of variation in species richness among contiguous reef sites was significantly different to those expected on the basis of the two null models simulating stochastic processes of colonisation and extinction. The random placement model, which simulated stochastic dynamics under conditions of spatially homogeneous recruitment, yielded a species-individuals curve with a significantly steeper slope than that based on observed data. This result parallels the consistent overestimation of species richness by rarefaction. Since both the random placement model and rarefaction procedure select individuals at random from the total pool of fish, it is not surprising that they yield similar results. If reef fish assemblages were organised entirely by spatially homogeneous lottery or recruitment-limited processes, the species-individuals relationships from the analyses of observed and randomised data would have been similar, and the observed numbers of species recorded from sites on contiguous and patchy reef would have been scattered on either side of the rarefaction curves.

The result of the comparison of observed data with data from the random placement model was similar to that obtained by Sale and Steel (1986). They found that the number of species expected on the basis of random placement (Model 1 in Sale and Steel 1986) was almost always greater than observed values on replicate patch reef sites. Their interpretation of this result was that random placement is not an appropriate model for all fish species, particularly given that some exhibit spatially and temporally heterogeneous distributions (Sale and Steel 1986). For this reason, we constructed a second null model, the group placement model, in which spatial variability in the distribution and abundance of fish species was preserved by randomising species counts among sites (as opposed to randomising individuals). The species-individuals relationships obtained from the group placement model differed markedly to both the relationship from observed data and that obtained from the random placement model (Fig. 1). Randomisation of species counts produced a flat species-individuals curve, indicating a relatively constant number of species among contiguous reef sites of the same area, regardless of the number of fish present. In contrast, the species-individuals relationship from the observed data was characterised by a significant positive slope, indicating that sites with low numbers of fish tended to contain less species than sites of the same area with high numbers of fish.

Based on the comparison of observed data with both null models and with rarefied estimates of species richness, there is little evidence to suggest that spatial variation in species richness is due to entirely stochastic processes. One possible explanation is that the variation in species richness reflects patterns of microhabitat selection among species. However, models of rarefaction residuals indicate that while some variation in species richness (relative to sample size) is related to habitat characteristics, the large majority remains unexplained by variability in habitat structure. We suggest that much of the unexplained variability may be due to species interactions within fish communities (e.g., competition and/or predation). The potential effects of positive or negative associations among species were not considered by either null model, and were not incorporated into regression models predicting spatial variation in species richness.

There are a number of mechanisms by which intra- or interspecific interactions can affect species richness. The most obvious is that interspecific competition may lead to competitive exclusion and thereby decrease species richness. Thus, certain combinations of closely competing species may be unlikely to coexist on a local habitat patch as competition leads to exclusion of one or more species. This idea is consistent with the findings that the observed levels of species richness were consistently less than those predicted by rarefaction, and that the species-individuals curves from the null models differed significantly from that based on observed data. In the computer-generated rarefaction process and in the null models there were no constraints on possible combinations of species. Thus, the analyses may have included combinations of species that are unlikely to persist in reality (Fager 1972, Williamson 1973), leading to overestimates of species richness (random placement model) or the lack of a relationship between numbers of species and numbers of individuals (group placement model).

Intra- and interspecific interactions can also modify patterns of larval settlement and thereby affect species richness. A number of studies have suggested that resident populations in local areas can facilitate larval settlement of conspecifics or deter settlement of other, possibly competitive species (Sweatman 1983, 1985, Jones 1987b, Booth 1992). Both interactions may act to reduce species richness by allocating available resources (e.g., food or space) to members of resident species. Interactive processes of this nature were not considered in the rarefaction procedure or the null models.

Predator-prey relationships may also influence spatial patterns in the structure of fish communities (Ayal and Safriel 1982, Hixon 1986, 1991, Hixon and Menge 1991, Hixon and Beets 1993, Carr and Hixon 1995, Beets 1997). Certain combinations of predators and prey may be unlikely to coexist at a local scale, leading to lower levels of species richness. Alternatively, the

presence of predators may increase species richness through 'keystone' predator-prey dynamics (Paine 1966).

If competitive and/or predator-prey interactions are important in organising fish communities on coral reefs, the question remains as to how high species richness is maintained? The answer may be related to the spatially heterogeneous nature of coral reef habitats. Within reefs, the reef habitat is fragmented, influenced by the patchy distributions of corals and/or large-scale disturbances (e.g., cyclone damage). Among reefs, individual reefs are isolated by open ocean, and resident fish populations are connected only by pelagic larval dispersal. In this spatially heterogeneous environment, fish species persist as metapopulations, at both the within- and among-reef scales. For rarer species, the existence of a large number of local populations (both within and among reefs) linked by migration (larval settlement and/or post-settlement movement) may compensate for the transient dynamics of local populations caused by competition, predation, and physical disturbance (see Richerson et al. 1970, DeAngelis and Waterhouse 1987, Hassell et al. 1994). Thus, for the entire metapopulation, spatial heterogeneity may act to reduce the directionality and severity of competitive and predator-prey interactions, leading to long-term species persistence and high species richness (see Huston 1979).

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